

The origin of the German populations of *Hilpertia velenovskyi* (Pottiaceae, Bryopsida): inferences from variation in the nuclear ITS region

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Abstract – *Hilpertia velenovskyi* is a continental-subarctic moss species, with a range extending from Ellesmere Island over Canada, Siberia, Mongolia and China to Eastern and South-Eastern Europe. The species is an element of cold loess steppes. Recently, *H. velenovskyi* was recorded as new from Eastern Germany in Saxony and in Western Germany in Rheinhessen. To clarify, whether the German populations are a result of recent spore dispersal or perhaps relicts from the last Ice Age, a molecular analysis of the nuclear ITS region has been undertaken. The results show a clear separation of the population from Rheinhessen from the other investigated populations, indicating a long isolation possibly since the last Ice Age or a recent spore long-distance dispersal. The population from Saxony clusters with populations from Hungary and Serbia and is thus part of a Central-European group.

Zusammenfassung – *Hilpertia velenovskyi* ist eine kontinental-subarktische Moosart, deren Areal von Ellesmere Island über Kanada, Sibirien in die Mongolei und China reicht und die Vorkommen im östlichen und südöstlichen Mitteleuropa hat. Sie ist eine Art der Kältesteppen auf Löß. Die westlichsten Vorkommen liegen in Sachsen in Ostdeutschland und Rheinhessen in Westdeutschland. Um zu klären, ob die rheinhessische, disjunkte Population von *Hilpertia* durch eine rezente Neuansiedlung über Sporenfernverbreitung stammt, oder aber autochton ist und dort eventuell schon seit der Eiszeit überdauert hat, wurde eine molekulare Untersuchung vorgenommen. Dabei wurden die genetischen Distanzen zwischen Populationen von *H. velenovskyi* aus Rheinhessen, Ungarn, Serbien und Zentralasien an Hand von Sequenzen der intern transkribierten Spacer 1 und 2 (ITS1/2 der nrDNA) bestimmt. Es zeigt sich, dass die Population aus Rheinhessen von den übrigen europäischen Populationen verschieden ist, was entweder bedeutet, dass diese Population seit langer Zeit, vermutlich seit der letzten Eiszeit, keinen Genaustausch mit den übrigen Vorkommen in Mitteleuropa hat und daher als Glazialrelikt zu werten ist. Eine andere Möglichkeit ist, dass diese Population durch Sporenausbreitung aus einem anderen Teil der Erde hierher gelangt ist. Die Population aus Sachsen clustert mit den übrigen Populationen aus Mitteleuropa und ist Teil dieser Gruppe.

Hilpertia velenovskyi / moss / Europe / phylogeography / ITS / neighbor-joining analysis

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INTRODUCTION

Many bryophyte species show transcontinental disjunct ranges, a pattern that is rather rare among vascular plants. Morphologically similar bryophyte populations that are widely allopatric can be genetically similar, as a result of either limited evolutionary potential or frequent gene flow by long-distance dispersal. Alternatively, phenotypically similar and disjunct populations of bryophytes may be genetically differentiated, a consequence of genetic isolation due to a lack of gene flow. Problems of genetic divergence of morphologically homogenous bryophytes give interesting insights into phylogeography of bryophytes (Bischler and Boisselier-Dubayle, 1997; Wyatt et al, 1997; Shaw and Allen, 2000; Shaw, 2001). One of the bryophyte examples with a very scattered range is *Hilpertia velenovskyi* (Schiffn.) Zand.

Hilpertia is a monospecific genus. It is based on material collected in the vicinity of Prague in the Czech Republic and described by Schiffner in 1893 as *Tortula velenovskyi* Schiffner. Later Zander (1989) gave the genus *Hilpertia*, based on the strongly recurved laminal margins forming a hollow tube of thin-walled and papillose cells. The species is characteristic of cold steppe habitats. The type locality remained for a long time the only known locality for this species. Some fifty years later, Boros (1944) found *H. velenovskyi* in North-Eastern Hungary. Subsequently Podpera (1954) recorded it from Serbia, Pilous (1958) from the Czech Republic and Waclawska (1958) and Kuc (1960) from Poland. Later, Pócs (1999) added many new localities for Hungary and neighbouring regions. Müller (2000) reported this species as new for Germany based on a collection from the vicinity of Dresden (Eastern Germany), and Frahm (2000) confirmed the presence of this species in Germany based on a collection from another loess cliff from Rheinhessen (Western Germany). The records by Dresden in Saxony is close to known localities of *H. velenovskyi* in Czech Republic, but the one in Rheinhessen is the westernmost locality in Europe and quite far away from any other continental population.

Firstly, it has been thought that *H. (Tortula) velenovskyi* is a European endemic species. However, another *Hilpertia* species (*Hilpertia scotteri* (R.H. Zander & Steere) R.H. Zander) was described from the Northwest Territories of Canada as *Tortula scotteri* R.H. Zander & Steere (Zander & Steere, 1978). Tan and Zhao (1997) treat *H. scotteri* as a synonym of *H. velenovskyi*, which extends the range of this species across the Northern Hemisphere and makes it even more scattered. During the last few decades, many new sites in the Northern Hemisphere were recorded (Bai 1987; Tung 1963; Sibiria: Ignatov & Afonina, 1992; China: Tan & Zhao, 1997; North-Canada: Zander, 1989; dry areas of British Columbia: McIntosh, 1989; Ellesmere Island: Mogensen & Zander, 1999).

Hilpertia velenovskyi is a continental-subarctic moss species, with a range from Ellesmere Island over Canada, Siberia, Mongolia and China to Eastern and South-Eastern Europe. The species is an element of cold loess steppes. The habitat of *Hilpertia* in Europe on dry and sunny loess cliffs, as well as the accompanying bryophyte species (species of *Aloina*, *Pterygoneuron*, *Crossidium* pp.) suggests a xerothermic species. For a map of the complete holarctic distribution see Müller (2000), which suggests a rather subarctic – continental range.

The westernmost European population are in Germany (Rheinhessen) and this disjunction raises the question about the origin of this population. The record near Dresden is not far from the localities in Czech Republic, whereas the

record from Rheinhessen is more than 500 km disjunct from the central and eastern European populations. There are principally two possibilities: First, the population in Rheinhessen is a result of a relatively recent dispersal from the population in Central and Southeast Europe, or long-distance dispersal from some extra European population. Secondly, we may also consider a long lasting separation of the population, which may even go back to the last glaciation, when *Hilpertia* could have been indigenous in the former loess steppe in Rheinhessen. The possibility that species could be overlooked is excluded since loess cliffs are small and ones of the best investigated habitats due to its extremely interesting cryptogamic flora.

To clarify the origin of *Hilpertia* in Germany and to infer relationships of selected populations of *H. velenovskyi*, a molecular study based on sequences of the internal transcribed spacer 1 and 2 was undertaken. Since *H. velenovskyi* is threatened species listed in European Red Data Book (ECCB, 1995), the understanding of its genetic diversity within the species is essential to develop strategies of collection, conservation and germplasm-formation. Genetic variation within a taxon is thought to be crucial for the long-term survival and continued evolution of populations or species (Franklin, 1980; Beardmore, 1983; Frankel, 1983; Huenneke, 1991). Thus, an accurate estimate of the level and distribution of genetic diversity of threatened and endangered species is an important element in proper conservation (Hamrick *et al.*, 1991; Shaal *et al.*, 1991; Chalmers *et al.*, 1992; Cardoso *et al.*, 1998; Kim *et al.*, 2005) However, due to status of species and scarcity of herbarium material, the data presented in this study should be considered as preliminary ones, until the implications for conservation rely on an extensive sampling of the populations.

MATERIAL AND METHODS

Hilpertia velenovskyi is protected by law in many countries, because of its rarity and vulnerability (e.g. Rajczy, 1990; Ochyra, 1992; Kučera & Vána, 2003; Sabovljević *et al.*, 2004). Only six samples were available or suitable based on age and size of the collection, for our study:

1. Hungary, Tolna County, Mezöföld, Dunakömlöd (Paks). On 6-20 m high, N exposed loess cliffs at the N end of Sánc-H. with rich cryptogamic vegetation at 110-130 m alt. 46°39.3'N, 18°52'E, *leg. S. & T. Pócs, G. Kís & A. Szabó.*
2. Germany, Saxony, Meissen NW:Elbhänge an der Karpfenschänke, südexpionierte Lösswände, *leg. F. Müller.*
3. China, Provinz Gansu, 40 km NW Lanzhou, 1820 m, Mergelhänge, 36°18.3'N, 103°38.5'E, *leg. B.Tan.*
4. Hungary, Tokaj, Donath, Nagykopasz area, 160-200 m, loess cliff, *leg. H. Kürschner.*
5. Germany, Rheinland-Pfalz, Rheinhessen Kr. Alzey, Naturschutzgebiet Steinkaute bei Dorn-Dürkheim, *leg. A. Oesau.*
6. Serbia, Vojvodina, Bačka, Titel plateau, Mošorin, loess cliff, *leg. M. Sabovljević.*

The Internal Transcribed Spacer 1 and 2 (ITS1/2) were used as molecular markers to infer the infraspecific variability. The DNA extraction and PCR protocols follow Stech and Frahm (2001) and Quandt *et al.* (2004). Alignment and tree formation followed the protocol by Borsch *et al.* (2003), using Align

(Hepperle, 2002) and PAUP4.0 (Swofford, 2001). For the determination of genetic differences, a comparison of nuclear ITS sequences based on uncorrected "p" distance was performed using the Neighbour joining - Method (Saitou and Nei, 1987). Gaps were treated as missing data.

RESULTS AND DISCUSSION

Nucleotide sequences were obtained for all six samples and deposited in EMBL Nucleotide Sequence Database with the accession numbers AJ973246, AJ973247, AJ973248, AJ973249, AJ973250 and AJ973251. A comparison of ITS sequences based on uncorrected "p"-distances suggests that the variation in sequences is not partitioned geographically, and hence that geographic origin is a poor predictor of genetic identity between two populations of *H. velenovskyi*.

The length of ITS varies between 760 to 831bp. The Chinese population has slightly more insertions and deletions (indels) compared to European. The GC content is equilibrated (53.21-54.63%). Such a high GC content for ITS in *Hilpertia* can be explained by its extremely xerophytic character. A higher GC content may result from adaptation to warm and arid habitats (in animals: Bernardi *et al.*, 1988 and in plants: Salinas *et al.*, 1988; Jobst *et al.*, 1998; Torres *et al.*, 1990; Jarret and Newman, 2000).

The alignment had a total length of 854 bp. The ITS1 region was highly variable with multiple indels, while ITS2 was less variable. The 5.8S rRNA gene had a constant length of 162 bp. The length variation observed in ITS was primarily attributable to the occurrence of a short (GC)_n, (GCC)_n and (CT)_n oligo-microsatellite in ITS1 and (AC)_n in ITS2.

The unrooted neighbor-joining tree for selected populations of *Hilpertia* (Fig. 1) shows that the Rheinhessen population from Western Germany is quite distinct genetically with the population Eastern Germany, Hungary or Serbia. The rather strong genetic isolation of the population from Western Germany (its ITS has 2 substitutions and 21 indels that distinguish it from other European populations) can be explained by a long period without gene exchange. This could be the case in a relict population of the last Ice Age, 13,000 years ago. It has to be considered, that *Hilpertia* could have been part of the flora in Central Europe during the last Ice Age. At that time, similar habitats were provided for the species as nowadays in Siberia or Ellesmere Island. Furthermore, loess was deposited in that time and loess cliffs persisted since that time, providing a constant habitat for bryophytes over the time.

Also, the presence of *H. velenovskyi* in Rheinhessen, can be explained by long-distance dispersal from somewhere inside or outside Europe. According to the tree and branch length of Chinese population (Fig. 1), Rheinhessen population is not related to the latter. This hypothesis would be supported by the fact that *Hilpertia* is known in Rheinhessen from only one locality and only recently discovered. On the other hand, long distance dispersal seems unlikely, since the next populations are in the Caucasus, Mongolia and Siberia, thus quite distant and situated against the prevailing wind system. However, this possibility should not be completely excluded since there are examples that long-distance dispersal in bryophytes are present where unexpected by vehicle of wind, storms, water flows and other means (Muñoz *et al.*, 2004). Species with highly disjunct

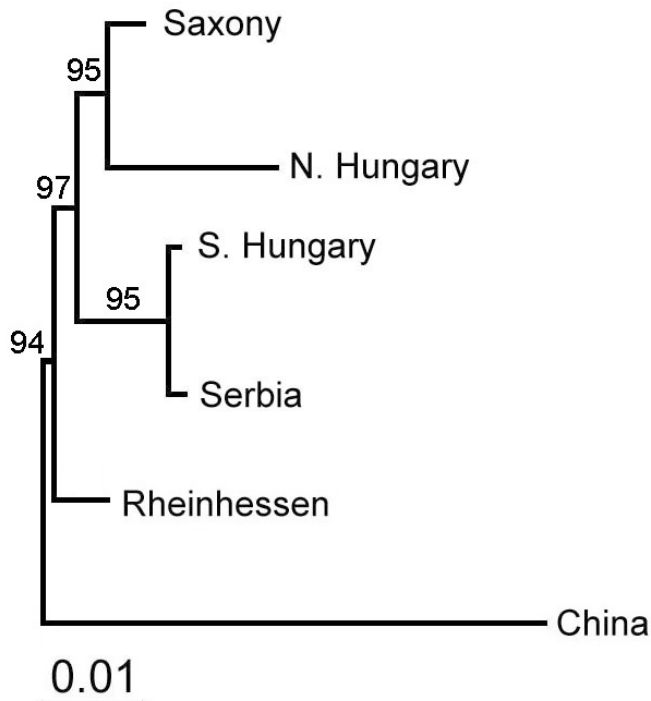


Fig. 1. The unrooted NJ tree for selected population of *Hilpertia velenovskyi* inferred by ITS nr DNA region. Bar scale indicates the inferred number of nucleotide substitutions.

distributions have generated controversy, however, because of long-distance migration is thought to be rare (Nathan, 2001). Several studies suggest that long-distance dispersal of spores may be more common than previously appreciated (James *et al.*, 2001; Skotnicki *et al.*, 2001; McDaniel and Shaw, 2003). However, empirical estimates of central parameters, such as rates of migration and colonization are still lacking (Husband and Barrett, 1996). In *Hilpertia* case, spores 10-12 μm in diameter and finely papillose, seems to be the most probable propagules for dispersal. Although the predominant means of dispersal of bryophytes on a local scale may be gametophyte fragments (Miller and Ambrose, 1976; During, 1997; McDaniel and Miller, 2000) or specialized asexual reproductive structure (Kimmerer, 1994), most long-distance dispersal is presumably accomplished by spores (Mogensen, 1981; Bremer and Ott, 1990; Miles and Longton, 1992). Consistent with some spores travelling long-distances, van Zanten (1978) found a strong positive correlation between spore longevity and size of distribution area. Moreover, the spore germination studies of van Zanten (1978) show that species with broad distribution often have spores tolerant of long storage and temperature extremes. The correlation between distributional area and spore tolerance may be underlain by additional habitat correlates such as substrate, which is the case with *H. velenovskyi* that is strictly restricted to specific habitats of loess cliffs (e.g. Pócs, 1999; Pócs *et al.*, 2002; Pócs *et al.*, 2004; Kürschner and Wagner, 2005).

A low rate variability of genetic data for *Bryum argenteum* Hedw. and *Ceratodon purpureus* (Hedw.) Brid. reveal large scale population structure, suggesting frequent long-distance dispersal in these species (Miller and McDaniel, 2004). It is likely that long-distance spreading in Rheinhessen from some other population occurred rather than that crypto-speciation started. Uit de Weerd *et al.* (2005) give molecular evidence in passive long-distance dispersal of some Greek land snail, explaining it by birds and by humans accidentally. Since, similar fauna and flora inhabit loess cliffs it can be expected such passive long-distance dispersal by some highly mobile organisms.

All other European populations are more or less related. The population tested from Vojvodina (Serbia) shows great similarity with south Hungarian population, while the north Hungarian population clusters with the population from East Germany. Two German populations are clearly genetically distinct and of different origin.

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REFERENCES

- BERNARDI G., MOUCHIROUD D. & GAUTIER C., 1988 — Compositional patterns in vertebrate genomes: Conservation and change in evolution. *Journal of molecular evolution* 28: 7-18.
- BISCHLER H. & BOISSELIER-DUBAYLE M.C., 1997 — Population genetics and variation in liverworts. *Advances in bryology* 6: 1-34.
- BREMER P. & OTT E. C.J., 1990 — The establishment and distribution of bryophytes in the woods of Ijsselmeerpolders, The Netherlands. *Lindbergia* 16: 3-18.
- BAI X.-L., 1987 — Primary report of the mosses in Inner Mongolia, China. *Acta scientiarum naturalium universitatis Intramongoliae* 18: 311-350.
- BEARDMORE J.A., 1983 — Extinction, survival and genetic variation. In: SCHOENWALD-COX C. M., CHAMBERS S. M., MACBRYDE B. & THOMAS L. (Eds), *Genetics and Conservation*. Menlo Park, CA, Benjamin-Cummings, pp. 125-151.
- BOROS A., 1944 — Florisztitai érdekességek a Bácskából. *Botanikai Közlemények* 41: 1-2.
- BORSCH T., HILU W., QUANDT D., WILDE W., NEINHUIS C. & BARTLOTT W., 2003 — Non encoding plastid *trnT-trnF* sequences reveal a well resolved phylogeny of basal angiosperms. *Journal of evolutionary biology* 16: 558-576.
- CARDOSO M.A., PROVAN W., POWELL J., FERRERAS P.C.G. & OLIVEIRA D. E., 1998 — High genetic differentiation among remnant populations of the endangered *Caesalpinia echinata* Lam. (Leguminosae-Caesalpinioideae). *Molecular ecology* 7: 601-608.
- CHALMERS K.J., WAUGH R., SPRENT J.I., SIMONS A.J. & POWELL W., 1992 — Detection of genetic variation between and within population of *Gliricidia sepium* and *G. maculata* using RAPD markers. *Heredity* 69: 465-472.
- DURING H.J., 1997 — Bryophyte diaspore banks. *Advances in bryology* 6: 103-134.
- ECCB, 1995 — *Red Data Book of European bryophytes*. Trondheim.
- FRAHM J.-P., 2000 — *Hilpertia velenovskyi* in Rheinhessen. *Limprichtia* 14: 27-30.
- FRANKEL O.H., 1983 — The place of management in conservation. In: SCHOENWALD-COX C.M., CHAMBERS S.M., MACBRYDE B. & THOMAS L. (Eds), *Genetics and Conservation*. Menlo Park, CA, Benjamin-Cummings, pp. 113-121.

- FRANKLIN E.R., 1980 — Evolutionary change in small populations. In: SOULÉ M. E. & WILCOX B.A. (Eds), *Conservation biology: an evolutionary-ecological perspective*. Sunderland, Sinauer, pp.135-150.
- HAMRICK J.L., GODT M.J.W., MURAWSKI D.A. & LOVELESS M.D., 1991 — Correlation between species traits and allozyme diversity: implication for conservation biology. In: FALK D.A. & HOLSINGER, K. E. (Eds), *Genetics and conservation of rare plants*. New York, Oxford University Press, pp. 75-86.
- HEPPERLE D., 2002 — *Alignment Editor Align*. Heidelberg.
- HUENNEKE L.F., 1991 — Ecological implications of genetic variations in plant populations. In: FALK D.A. & HOLSINGER, K.E. (Eds), *Genetics and conservation of rare plants*. New York, Oxford University Press, pp. 31-44.
- HUSBAND B.C. & BARRETT S.C.H., 1996 — A metapopulation perspective in plant population biology. *Journal of Ecology* 84: 461-469.
- IGNATOV M.S. & AFONINA O.M., 1992 — Checklist of the mosses of the former USSR. *Arctoa* 1: 1-85.
- JAMES T.Y., MONCALVO S.L. & VILGALIS R. 2001 — Polymorphism at the ribosomal DNA spacer and its relation to breeding structure of the widespread mushroom *Schizophyllum commune*. *Genetics* 157: 149-161.
- JARRET R.L. & NEWMAN M., 2000 — Phylogenetic relationships among species of *Citrullus* and the placement of *C. rehmi* De Winter as determined by Internal Transcribed Spacer (ITS) sequence heterogeneity. *Genetic resources and crop evolution* 47: 215-222.
- JOBST J., KING K. & HEMLEBEN V., 1998 — Molecular Evolution of Internal Transcribed Spacers (ITS1 and ITS2) and phylogenetic relationships among species of the family Cucurbitaceae. *Molecular phylogenetics and evolution* 9(2): 204-219.
- KIM S-C., LEE C. & SANTOS GUERRA A., 2005 — Genetic analysis and conservation of the endangered Canary Island woody sow-thistle, *Sonchus gandogeri* (Asteraceae). *Journal of plant research* 118: 147-153.
- KIMMERER R.W., 1994 — Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tertraphis pellucida*. *The bryologist* 97: 20-25.
- KUC M., 1960 — La distribution géographique de *Tortula velenovskyi* Schiffner. *Revue bryologique et lichénologique* 29: 92-96.
- KUČERA J. & VÁŇA J., 2003 — Check- and Red List of bryophytes of the Czech Republic (2003). *Preslia* 75: 193-222.
- KÜRSCHNER H. & WAGNER D., 2005 — Phytosociology and life strategies of a new loess slope bryophyte community from N China (Gansu), including *Crossidium laxefilamentosum* new to China. *Nova hedwigia* 81 (1-2): 229-246.
- McDANIEL S.F. & SHAW A.J., 2003 — Phylogeographic structure and cryptic speciation in the trans-Antarctic moss *Pyrrhobryum mnioides*. *Evolution* 57: 205-215.
- McDANIEL S.F. & MILLER N.G., 2000 — Winter dispersal of bryophyte fragments in the Adirondack Mountains, New York. *The bryologist* 103: 592-600.
- McINTOSH T.T., 1989 — Bryophyte records from the semi-arid steppe of north-western North America, including four species new to North America. *The bryologist* 92: 356-362.
- MILES C.J. & LONGTON R.E., 1992 — Deposition of moss spores in relation to distance from parent gametophytes. *Journal of bryology* 17: 355-368.
- MILLER N.G. & AMBROSE L.J.H., 1976 — Growth in culture of wind blown bryophyte gametophyte fragments from arctic Canada. *The bryologist* 79: 55-63.
- MILLER N.G. & McDANIEL S.F., 2004 — Bryophyte dispersal inferred from colonization of an introduced substratum on Whiteface Mountain, New York. *American journal of botany* 91 (8): 1173-1182.
- MOGENSEN G.S., 1981 — The biological significance of morphological characters in bryophytes: the spore. *The bryologist* 84: 187-207.
- MOGESEN G.S. & ZANDER R.H., 1999 — *Hilpertia velenovskyi* (Musci, Pottiaceae) new to the Arctic from Ellesmere Island, Northeastern Canada. *The bryologist* 102: 753-755.

- MÜLLER F., 2000 — Das Laubmoos *Hilpertia velenovskyi* (Schiffn.) Zander (Pottiaceae, eine für die Flora Deutschlands neue Art. *Limprichtia* 14: 49-58.
- MUÑOZ J., FELICÍSIMO A.M., CABEZAS F., BURGAS A.R. & MARTÍNEZ I., 2004 — Wind as a long-distance dispersal vehicle in the southern hemisphere. *Science* 304: 1144-1147.
- NATHAN R., 2001 — Dispersal biogeography. In: Levin, S.A. (Ed), *Encyclopedia of biodiversity II*. New York, USA, Academic Press, pp. 127-152.
- OCHYRA R., 1992 — *Czerwona lista mchów zagrożonych Polsce (Red list of threatened mosses in Poland)* Krakow, Polish Academy of Sciences, pp. 79-85.
- PILOUS Z., 1958 — Fragmenta bryologica. *Preslia* 30: 31-40.
- PÓCS T., 1999 — A löszfalak virágtalan növényzete I. Orografikus sivatag a Kárpát-medencében. (Studies on the cryptogamic vegetation of loess cliffs, I. Orographic desert in the Carpathian Basin). *Kitaibelia* 4(1): 143-156.
- PÓCS T., GOIA I., KIS G., ORBÁN S., SASS-GYARMATI A. & VAN ZANTEN B.O., 2002 — *Hilpertia velenovskyi* (Schiffn.) Zander and other pottoid mosses (Bryophyta) new to Romania. Studies on the cryptogamic vegetation of loess cliffs, IX. *Contributii botanice Gradina Botanica, A. Borza Cluj-Napoca* 37: 13-24.
- PÓCS T., SABOVLJEVIĆ M., PUCHE F., SEGARRA-MORAGUES J.G., GIMENO C. & KÜRSCHNER H., 2004 — *Crossidium laxefilamentosum* Frey and Kürschner (Pottiaceae), new to Europe and to North Africa. (Studies on the cryptogamic vegetation on loess cliffs, VII.) *Journal of bryology* 26: 113-124.
- PODPĚRA J., 1954 — *Conspectus Muscorum Europaeorum*. Prag.
- QUANDT D., HUTTUNEN S., STREIMANN H., FRAHM J.-P. & FREY W., 2004 — Molecular phylogenetics in the Meteoriaceae s.str.: focusing on the genera *Meteorium* and *Papillaria*. *Molecular phylogenetics and evolution* 32: 435-461.
- RÁJČZY M., 1990 — Mohák-Bryophyta. In: Rakonczai Z. (Ed.), *Vörös könyv*. Budapest, Akadémiai Kiadó, pp. 322-325.
- SABOVLJEVIĆ M., CVETIĆ T. & STEVANOVIĆ V., 2004 — Bryophyte Red List of Serbia and Montenegro. *Biodiversity and conservation* 13: 1781-1790.
- SAITOU N. & NEI M., 1987 — The neighbour-joining method: a new method for reconstructing phylogenetic trees. *Molecular biology and evolution* 4(4): 406-425.
- SALINAS J., MATASSI G., MONTERO L.G. & BERNARDI G., 1988 — Compositional compartmentalization and compositional patterns in the nuclear genomes of plants. *Nucleic acid research* 16: 4269-4285.
- SHAAL B.A., LEVERICH W.J. & ROGSTAD S.H., 1991 — A comparison of methods for assessing genetic variation in plant conservation biology. In: FALK D.A. & HOLSINGER K.E. (Eds), *Genetics and conservation of rare plants*. New York, Oxford University Press, pp. 123-134.
- SHAW A.J. & ALLEN B.H., 2000 — Phylogenetic relationships, morphological incongruence and geographic speciation in the Fontinalaceae (Bryophyta). *Molecular systematics and evolution* 16: 225-237.
- SHAW A.J., 2001 — Biogeographic patterns and cryptic speciation in bryophytes. *Journal of biogeography* 28: 253-261.
- SKOTNICKI M.L., SELKIRK P.M., BROADY P., ADAM K.D. & NINHAM, J.A., 2001 — Dispersal of the moss *Campylopus pyriformis* on geothermal ground near summits of Mount Erebus and Mount Melbourne, Victoria Land, Antarctica. *Antarctic science* 13: 280-285.
- STECH M. & FRAHM J.-P., 2001 — The systematic position of *Ochyraea tatrensis* (Hypnobartelliaceae, Bryopsida) based on molecular data. *The bryologist* 104: 199-203.
- SWOFFORD D.L., 2001 — PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland.
- TAN B.C. & ZHAO J.C., 1997 — New moss records and range extensions of some xeric and alpine moss species in China. *Cryptogamie, Bryologie-Lichénologie* 18: 207-212.
- TORRES R.A., GANAL M. & HEMLEBEN V., 1990 — GC balance in the internal transcribed ITS1 and ITS2 of nuclear ribosomal RNA genes. *Journal of molecular evolution* 30(2): 171-181.

- TUNG C.-K., 1963 — Notes on some xerophytic mosses in China. *Acta scientiarum naturalium universitatis Intramongoliae* 6: 173-184.
- UIT DE WEERD D.R., SCHNEIDER D. & GITTENBERGER E., 2005 — The provenance of the Greek land snail species *Isabellaria pharsalica*: molecular evidence of recent passive long-distance dispersal. *Journal of biogeography* 32: 1571-1581.
- VAN ZANTEN B.O., 1978 — Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern Hemisphere. *Journal of the Hattori botanical laboratory* 44: 455-482.
- WACLAWSKA Z., 1958 — *Tortula velenovskyi* Schiffner w Polsce. *Fragmenta floristica et geobotanica* 3 (2): 181-185.
- WYATT R., ODRZYKOSKI I.J. & KOPONEN T., 1997 — *Mnium orientale* sp. nov. from Japan is morphologically and genetically distinct from *M. hornum* in Europe and North America. *The Bryologist* 100: 226-236.
- ZANDER R.H. & STEERE W.C., 1978 — *Tortula scotteri* sp. nov. from the Northwest Territories of Canada. *The bryologist* 81: 463-467.
- ZANDER R.H., 1989 — Seven new genera in Pottiaceae (Musci) and a lectotype for *Syntrichia*. *Phytologia* 65: 424-436.